Environment and the Distribution of Microfungi in a Hawaiian Mangrove Swamp[1]

BENNY K. H. LEE[2] AND GLADYS E. BAKER[2]

EXTENSIVE INVESTIGATIONS of the ecological relationships of soil microfungi with soil types, pH, moisture, horizon, temperature, and macrovegetation have been published (Parkinson and Waid, 1960; Alexander, 1961; and Burges and Raw, 1967). It is a well-established principle that soil fungi are influenced by specific soil environments. Mangroves occupy a littoral habitat, characterized almost invariably by salt or brackish water and coastal silt. The microfungi in the mangrove swamp must be able to tolerate the conditions characteristic of this special ecosystem. Their distribution in particular may be affected by the salinity of the mangrove swamp (Swart, 1958; and Kohlmeyer, 1969). Tolerance to different salinity levels may correlate with temperature levels as demonstrated by Ritchie (1957, 1959) in a series of *in vitro* experiments. For those microfungi occurring in association with the mangrove roots, it is also necessary to consider the influence of the root itself and the rhizosphere effect. The latter is designated as the region of soil subject to the immediate influence of plant roots (Katznelson, Lochhead, and Timonin, 1948).

A series of *in vitro* tests was undertaken to determine the relationship of environmental conditions to the distribution of fungi in the Heeia mangrove swamp on Oahu, Hawaii. Test fungi were selected from isolates obtained from brackish to marine habitats and included species growing on roots of *Rhizophora mangle* L. and in mangrove (*R. mangle*) swamp soil. Studies were designed to determine levels of salinity tolerance for each species and the combined effect of temperature and salinity on the growth rate of these fungi. Further study concerned the effects of mangrove root extract and mangrove swamp soil extract on fungal growth.

MATERIALS AND METHODS

Test Organisms

Five fungi were selected from different salinity levels in the Heeia mangrove swamp. All were used in the salinity tolerance tests; the first three were used to determine the interaction of salinity and temperature.

ISOLATES FROM HIGH SALINITY SITES: *Robillarda rhizophorae* Kohlm. was isolated from submerged dead prop roots of *Rhizophora mangle* L. at the seaward side of Heeia swamp near the fishpond. The location corresponds to station 5 of Walsh (1967). Salinity readings obtained monthly between August 1961 and November 1962 varied from 0.73 to 29.34 ‰ (low tide) and from 18.88 to 41.9 ‰ (high tide) according to Walsh. Soil salinity at the collecting site was 30 ‰ on 29 March 1970. *Dendryphiella salina* (Sutherland) Pugh & Nicot was isolated from the rhizosphere soil of *Rhizophora mangle* seedlings at the same location as *Robillarda rhizophorae.*

ISOLATES FROM LOWER SALINITY (BRACKISH) SITES: *Trichoderma viride* Pers. was isolated from the mangrove swamp soil in the seaward area where soil salinity tests made on 8 July 1968 and 2 November 1969 read approximately 14.0‰ (Lee, 1971). *Penicillium vermiculatum* Dangeard and *Circinella simplex* Van Tieghem were isolated from the mangrove swamp soil at the inland area where soil salinity tests made on 8 July 1968 and 2 November 1969 read 5.2 and 5.9 ‰, respectively.

Robillarda rhizophorae, Dendryphiella salina, and *Trichoderma viride* were the three species selected as the test organisms for the

---

[1] Based on part of a dissertation presented by the senior author in partial fulfillment of the requirements for the Ph.D. degree in botanical sciences at the University of Hawaii. This investigation was supported by Public Health Service grant no. GM 15198 from the National Institutes of Health. Manuscript received 9 June 1971.

[2] University of Hawaii, Department of Botany, Honolulu, Hawaii 96822.

study of the combined effect of salinity and temperature.

To study the influence of mangrove root and soil extracts on growth, we used six species and two strains as the test organisms, namely *Robillarda rhizophorae,* a mangrove root isolate; *Circinella simplex*, *Pycnidiophora multispora* (Saito & Minoura) Thompson & Backus, and *Fusarium oxysporum* Schlechtendahl, all mangrove soil isolates; and both mangrove root (*Rhizophora mangle*) and soil isolates of *Cylindrocladium parvum* Anderson and *Trichoderma viride.*

Basal Medium and Culturing Methods

The basal medium was a broth based on Emerson's YpSs agar (Difco 0739) which contained, per liter: yeast extract, 4 g; starch, 15 g; dipotassium phosphate, 1 g; magnesium sulfate, 0.5 g.

Natural seawater with a salinity of 36 ‰, as measured by an electrical conductivity method (Chapman and Pratt, 1961), was used for the salinity tolerance and temperature study. Media of varying salinity levels were achieved either by dilution with distilled water or by partial evaporation and reconstitution to desired strengths. The final salinity concentrations were 1.0 (with distilled water), 6, 12, 18, 27, 36, and 72 ‰. The pH of the media varied from 6.8 to 7.1.

Each of the fungi to be tested was grown in triplicate in 25 ml of liquid medium in 125-ml Erlenmeyer flasks and placed on a New Brunswick gyratory shaker (200 rpm) at room temperature (24° to 26° C) for 7 days. Flasks were inoculated aseptically with three loops of spore suspension prepared in sterile distilled water. After seven days mycelia from each flask were harvested by suction filtration on tared filter paper, washed in distilled water, dried at 85° C for 2 days, and weighed. The measurement of growth was recorded as the mean of three replicates and its standard error. The salinity tolerance test for *Robillarda rhizophorae* was repeated to confirm the maximum level of salinity tolerance.

The combined effects of salinity and temperature on the growth of *Robillarda rhizophorae, Dendryphiella salina,* and *Trichoderma viride* were studied in petri dish culture using Emerson's YpSs agar (Difco 0739) and seawater to give salinity concentrations of 6, 12, 18, 27, 36, and 72 ‰. Each petri dish was inoculated at the center with a loopful of spore suspension prepared in sterile distilled water. Cultures were incubated at 10, 20, 25, 30, and 37° C for 12 days except *T. viride* which was grown for 4 days. Growth was recorded in terms of colony diameter, measured from the hyphal tips on one advancing edge to the opposite edge. All experiments were performed in triplicate.

Root or soil extract was used in the basal medium as 500 ml per liter to determine the effects of mangrove root and soil extracts on fungal growth. The basal medium served as the control medium. Mangrove root extract was prepared from the roots of 1-year-old mangrove seedlings. The roots were washed in running water, air-dried for 1 day, and weighed. About 200 g of dried roots were soaked in 1 liter of distilled water for 3 days. The solution then was filtered through cheesecloth and Whatman filter paper no. 1. The pH of the root extract was adjusted from the initial pH 5.7 to pH 7.0 by 1 N NaOH. Half of the extract was sterilized by passage through a 0.45-μ Millipore filter and the remainder by autoclaving at 15 psi and 121° C for 20 minutes. Soil extract was prepared by adding 1 kg of mangrove (*Rhizophora mangle*) swamp soil to 1 liter of tap water. The slurry was filtered repeatedly until clear and the filtrate brought up to 1 liter with tap water. Unfortunately, the extract would not pass a 0.45-μ Millipore filter so it was autoclaved at 15 psi and 121° C for 20 minutes after adjustment of the pH to 7.0 from the initial pH 6.8 by 1 N NaOH. Methods of inoculation and the measurement of fungal growth were the same as those used in the salinity tolerance study.

RESULTS AND DISCUSSION

Salinity Tolerances and Effect of Temperature

The growth responses of the five fungi subjected to various concentrations of seawater at 24° to 26° C are shown in Fig. 1. The fungi which came from three different habitats

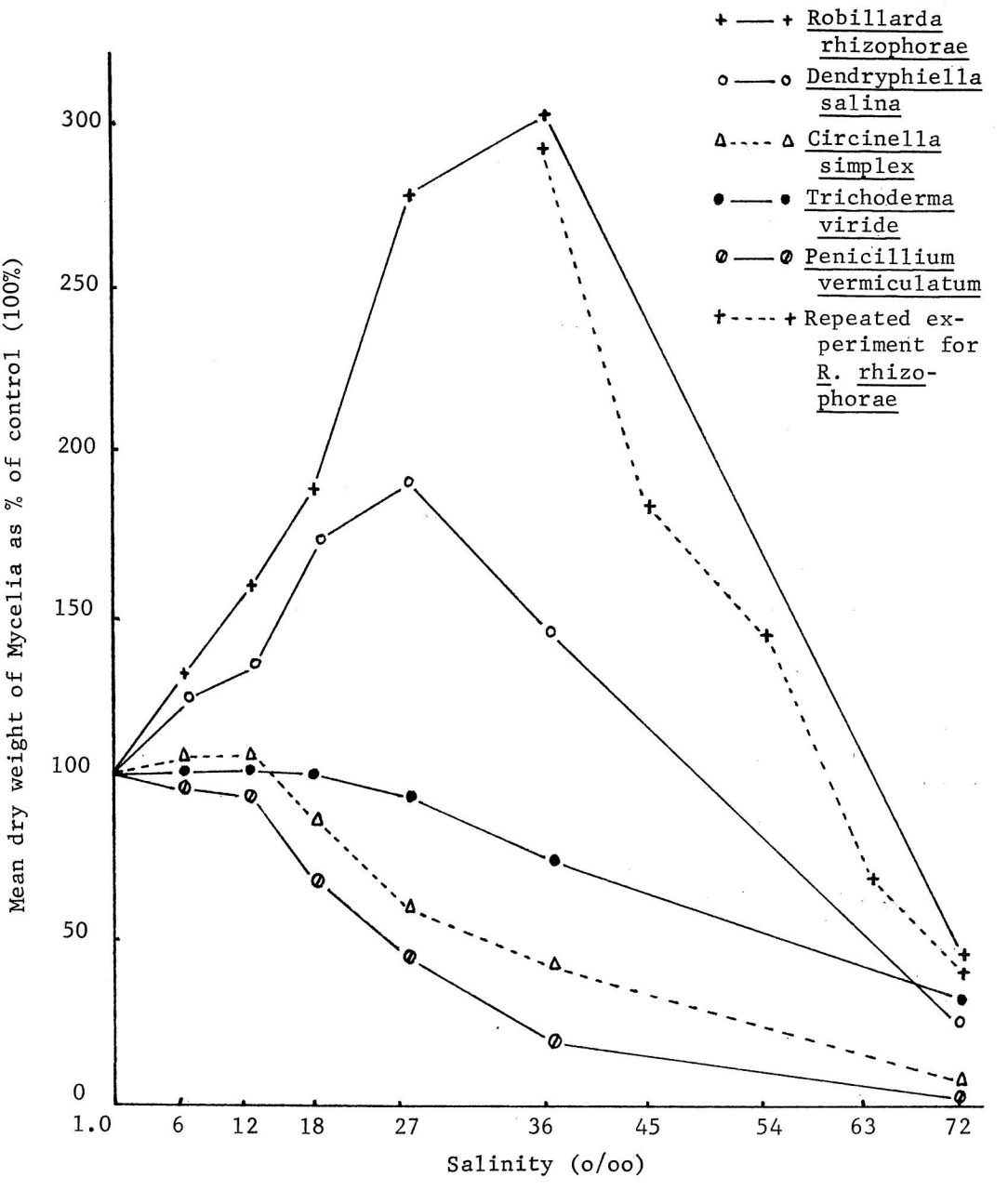

FIG. 1. Growth responses of five fungi to various concentrations of seawater (salinity 36 ‰) obtained by appropriate dilution with distilled water or concentration of natural seawater at room temperature (24°–26° C), measured as dry weight of mycelia after 7 days.

roughly can be grouped as two from a high-salinity area (30 ‰) and three from lower salinities corresponding to brackish situations (5.2 to 14 ‰). The growth of all the fungi except *Penicillium vermiculatum* was stimulated at low salinity (6 ‰), although *Trichoderma viride* was stimulated only slightly. The three brackish isolates responded with similar growth

patterns as did the two isolates from higher salinities.

Robillarda rhizophorae and *Dendryphiella salina* exhibited a rather intensive response to varying concentrations of seawater. They showed increased growth from 6 to 27 ‰ salinity with maximum growth for *Robillarda rhizophorae* at 36 ‰. Above 36 ‰, growth was sharply reduced. These fungi were reproductive in the distilled-water medium and lower concentrations of seawater medium (6 to 27 ‰). No fruiting structures were seen at 36 and 72 ‰ of seawater agar medium after 2 weeks. These salinities are in excess of the natural habitat where these fungi do fruit. *Robillarda rhizophorae* and *Dendryphiella salina* have been considered marine fungi (Kohlmeyer, 1969; Pugh and Nicot, 1964). The increased dry weight of fungi grown in seawater medium may result from a more favorable ionic environment. Gray, Pinto, and Pathak (1963) ascribed such mycelial increase to the magnesium ion in seawater. Jones and Jennings (1964) indicated that the growth of some marine fungi, notably *Dendryphiella salina* and *Lulworthia* species, was favored in an ionic environment such as sodium. Sodium ions stimulate dry weight production at low concentrations but inhibit it at high concentrations. The rate of utilization of nutrients may be increased by a cationic environment. However, in the present study, the growth of these two isolates, *Robillarda rhizophorae* and *Dendryphiella salina*, was stimulated at lower salinity levels and inhibited between 36 and 72 ‰. In a repeated experiment on *Robillarda rhizophorae* the data confirmed previous results. Its maximum tolerance is 36 ‰ and growth at concentrations above that decreases sharply (Fig. 1).

In vitro growth responses of the three brackish water isolates correlated well with conditions of their habitat. *Trichoderma viride* produced good growth at 6, 12, and 18 ‰ but slightly reduced growth at 36 ‰ and less than 50 percent at 72 ‰ of salinity. In nature the soil salinity level of the location for this species was 14.0 ‰. *Penicillium vermiculatum* and *Circinella simplex* are very salt-sensitive organisms. *Penicillium vermiculatum* and *Circinella simplex* exhibited reduced growth at 6 ‰ and 18 ‰, respectively. In nature, the soil salinity level at the location of these two species was 5.2 to 5.9 ‰. The dry weight of mycelia of *Penicillium vermiculatum* at 27 ‰ and *Circinella simplex* at 36 ‰ was reduced to less than half that of the control. *Penicillium vermiculatum* and *Circinella simplex* occurred abundantly in the less saline zone (inland zone) but were absent (*C. simplex*) or present only in low numbers (*Penicillium vermiculatum*) in the saline zone of the mangrove swamp (Lee, 1971). The brackish water isolates grew best in, or were able to tolerate, the lower concentration of seawater, whereas the seawater isolates grew best in, or could tolerate, the higher concentration of seawater.

The responses of *Robillarda rhizophorae, Dendryphiella salina,* and *Trichoderma viride* to various conditions of salinity and temperature are shown in Figs. 2, 3, and 4. In general these fungi grew poorly or did not grow at either 10° or 37° C. Temperatures of 25° and 30° C produced maximum growth. Within the conditions of the experiment, the optimum temperature for growth was 25° C. Since these three fungi were isolated from a tropical climate, it is not unexpected that they exhibited

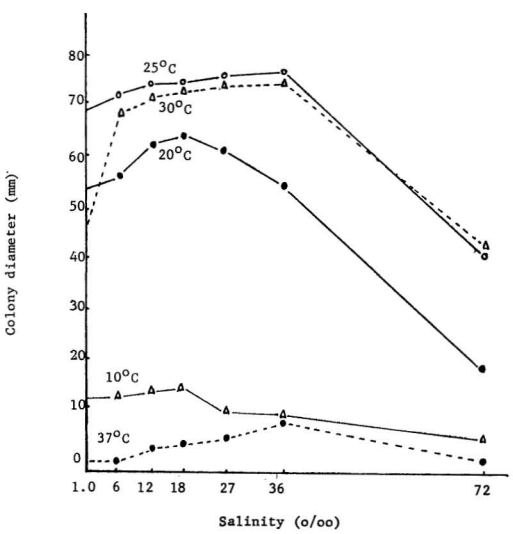

FIG. 2. Growth of *Robillarda rhizophorae* at different temperatures and various seawater salinities after 12 days.

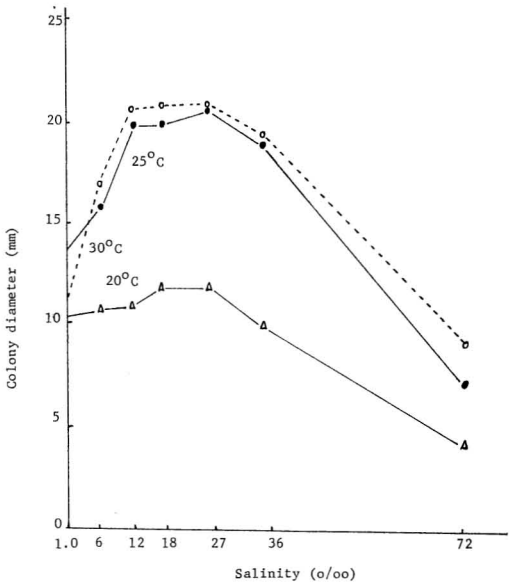

FIG. 3. Growth of *Dendryphiella salina* at different temperatures and various seawater salinities after 12 days.

little or no tolerance to a low temperature environment.

Robillarda rhizophorae displayed a typical "*Phoma*-pattern" growth rate by Ritchie's definition (1957), with the best low-temperature growth at low-seawater salinity, and the best high-temperature growth at high salinity (Fig. 2). At 10° and 20° C the peak growth range was 12 to 18 ‰. Comparatively, the fungus grew better in low salinity (6 to 18 ‰) than in high salinity. At 30° C, the peak occurred from 27 to 36‰. At 37° C, the fungus displayed no growth at 6 ‰ and peak growth at 36 ‰. Some growth was maintained at 72 ‰.

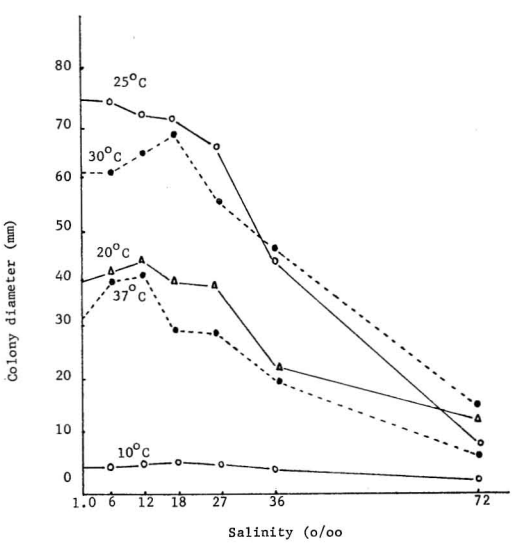

FIG. 4. Growth of *Trichoderma viride* at different temperatures and various seawater salinities after 4 days.

Dendryphiella salina did not grow at 10° and 37° C. The growth rate of this fungus was very slow but differences in colony diameters were measurable. Growth was faster at higher temperatures (25° and 30° C) than at low temperature (20° C) (Fig. 3), but the "*Phoma* pattern" of growth was not observed.

Trichoderma viride, a fast-growing organism, displayed mycelial development after 1 day and mycelia almost covered the plate after 7 days. After 4 days, the fungus grew very poorly at 10° C and salinity seemed to have little effect on its growth rate at this temperature (Fig. 4). However, at 20°, 25°, 30°, and 37° C, *T. viride* showed better growth in low-salinity (6 and 18‰) media than at the high-salinity (27, 36, and 72‰) media. This fungus could tolerate high salinity (up to 72 ‰) and high temperature (37° C), which suggests that it has the ability to grow well at temperatures and salinities which might obtain in tropical marine habitats.

Temperature is considered an important natural factor governing the geographical distribution of fungi (Bisby, 1943). It follows that fungi isolated from habitats with different temperatures will grow better *in vitro* at temperatures similar to those of their sources.

Barghoorn and Linder (1944), working with some lignicolous fungi from the temperate Atlantic Ocean, reported that the most favorable temperature range for growth of those marine fungi lies between 22.5° and 27.5° C. In the present *in vitro* study, the optimum temperature was 25° C for *Robillarda rhizophorae* and *Trichoderma viride*. *Dendryphiella salina* did equally well at 30° C. Salinity levels for these optima were 36 ‰, 6 ‰, and 27 ‰, respectively.

Ritchie (1957, 1959) demonstrated that

water temperature and salinity have a combined effect on the growth rate of some fungi such as *Phoma* sp., *Pestalotia* sp., and *Curvularia* sp. for which a low salinity must accompany low temperature and high salinity a high temperature to obtain optimum results. In this study, *Robillarda rhizophorae* exhibited the same phenomenon of growing better at a high temperature at increased salinity in the medium. Temperature altered salinity tolerance but salinity level did not change the optimum temperature for the fungal growth. TeStrake (1959), studying the response of *Dictyuchus monosporus* to changes of salinity and temperature in laboratory culture, suggested that a limited nutrient supply may be responsible for its distribution. However, in a study of the effects of osmotic and nutritional variation on growth of *Zalerion eistla, in vitro,* Ritchie and Jacobsohn (1963) indicated that nutrient quantity alone does not determine the general salinity-temperature relation. They suggested that the effects of temperature or salinity or both together appeared to be a matter of osmotic pressure of the surrounding medium.

In a study of the ecology of soil microfungi in this same mangrove swamp, Lee (1971) found that the salinity of seawater is one of the factors limiting the distribution of some fungi in the mangrove swamp. Results of this study suggest that salinity affects the growth of mangrove fungi and, in turn, their distribution. Fungi isolated from the seaward area grow best *in situ* because they can tolerate higher concentrations of seawater, whereas fungi sensitive to higher salinities grow best in the inland area. The natural distribution of these fungi correlates with the *in vitro* findings for salinity tolerances.

Effects of Mangrove Root and Soil Extracts

The growth of six species and two strains tested in soil and root extracts is shown in Table 1. The root extract was assumed to simulate root excretions and, therefore, may be regarded as simulating the "rhizosphere effect." The root extract and soil extract affected the selected microfungi differently.

Robillarda rhizophorae, a mangrove root isolate, was stimulated by both autoclaved and filter-sterilized root extracts made from the same mangrove, *Rhizophora mangle.* The dry weights of the mycelia grown with root extracts were twice those of the control. This suggested that the mangrove root extract contained one or several growth substances which accelerated growth. Autoclaving the root extract intensified the stimulation of the fungal growth more than did filter-sterilizing the root extract. Heat sterilization could activate growth factors pres-

TABLE 1

GROWTH OF MANGROVE-ASSOCIATED FUNGI AFTER 7 DAYS IN EMERSON YPSS BROTH SUPPLEMENTED WITH EXTRACTS OF SOIL AND ROOTS

SPECIES	SOURCE	CONTROL (BASAL MEDIUM)*	DRY WEIGHT AS % OF CONTROL**		
			MANGROVE SOIL EXTRACT	MANGROVE ROOT EXTRACT	
			AUTOCLAVED	AUTOCLAVED	FILTER STERILIZED
Robillarda rhizophorae	root	211	117.0	224.6	192.4
Pycnidiophora multispora	soil	87	106.8	77.0	66.6
Circinella simplex	soil	224	102.3	97.6	86.0
Fusarium oxysporum	soil	231	118.6	109.9	105.1
Trichoderma viride	root	325	99.3	103.6	100.0
	soil	312	100.3	100.1	99.0
Cylindrocladium parvum	root	151	121.8	133.0	129.8
	soil	160	123.7	113.0	108.1

* Dry weight of mycelia (in mg) recorded as the mean of three replicates.
** Control = 100.

ent in root extract or inactive inhibitory factors. Soil extract stimulated the growth of this fungus only slightly.

Pycnidiophora multispora and *Circinella simplex* were isolated from the mangrove soil but were not present on the mangrove root. Growth rates of these fungi were slightly increased by the autoclaved soil extract—yields ranging from 6.8 percent to 2.3 percent in excess of the control (Table 1). Soil extract may contain some nutrients or other growth factors which increase fungal growth. James (1958) indicated that a soil extract contains unidentified growth factors with a higher level of nutrients in heated extract than in unheated extract. However, the root extract inhibited the growth of these two fungi. One possible explanation is that inhibition is due to the presence of tannin in the mangrove plant inasmuch as it is known to contain a great amount of tannin (Morton, 1965). Mangrove root extract used in this experiment was tested for the presence of tannin by a ferric sulfate test after Jensen (1962); this showed that mangrove root extract contains an abundance of tannin. There is evidence that tannin can inhibit fungal growth (Vaartaja, 1960; Cowley and Whittingham, 1961; Lewis and Papavizas, 1967). Further study of the relationship between tannin and fungal growth is required to clarify this point. The filter-sterilized root extract produced greater inhibition than the autoclaved extract. This may mean that the inhibitory action of the root extract was reduced by the heat, as suggested for the same effect noted in the growth of the root isolate, *Robillarda rhizophorae.*

Fusarium oxysporum was isolated from the soil but its occurrence on the mangrove root in Heeia swamp has been reported (Lee, 1971). Its growth was favored in both the soil and root extracts, but stimulation by the soil extract was approximately 10 percent more than that of the root extract.

Trichoderma viride and *Cylindrocladium parvum* were tested using isolates from both the mangrove root and soil. The growth rates of root and soil strains of *Trichoderma viride,* in both root and soil extracts, were almost the same as in the control. The root and soil strains of *Cylindrocladium parvum* were stimulated by both soil and root extracts (Table 1). The root isolate grew better than the soil isolate in the root extract, whereas the soil isolate grew better than the root isolate in the soil extract. Each isolate represents a tolerant strain with physiological adaptation to its habitat.

In a previous study Lee (1971) suggested that the fungi living in the mangrove community are governed by the macrovegetation. The mangrove plant may play a role in microfungal population as expressed both in density and in species composition. The results of this *in vitro* study showed that the "rhizosphere effect" on the fungal growth was selective. It could be selectively stimulatory for some fungi but selectively inhibitory for others. Generally, fungi isolated from the mangrove root grew best in the mangrove-root-extract medium whereas fungi isolated from the soil grew best in soil-extract medium.

SUMMARY

Growth rates of five fungi, *Robillarda rhizophorae, Dendryphiella salina, Trichoderma viride, Penicillium vermiculatum,* and *Circinella simplex,* isolated from the mangrove habitat were studied using a range of seawater salinities from 6 to 72 ‰. The combined effects of temperature and salinity on the growth rates of *Robillarda rhizophorae, Dendryphiella salina,* and *Trichoderma viride* were considered. *Robillarda rhizophorae* and *Dendryphiella salina* exhibited tolerance to high salinity. Maximum growth for both *Robillarda rhizophorae* and *Dendryphiella salina* was obtained at salt concentrations approximating those of their habitat. *Trichoderma viride* was shown to have a brackish habitat response, producing maximum growth at 18 ‰. *Penicillium vermiculatum* exhibited the most sensitive response to salinity. When salinity of the medium was increased above the level of its natural habitat (5.4 ‰), its growth was significantly decreased. *Circinella simplex* displayed a similar but less marked response. The fungi isolated from the less saline area grew best or were able to tolerate only lower concentrations of seawater, whereas the saline isolates grew best or could tolerate the high salinity of natural seawater. It may be

concluded that salinity is a controlling factor for the distribution of some of the fungi in the mangrove swamp.

Temperature plays an important role in the development of fungi. All three fungi tested either showed poor growth or no growth at 10° C and 37° C. The optimum temperature for the growth of these fungi was 25° C. *Robillarda rhizophorae* showed a typical "*Phoma*-pattern" growth rate with the best low-temperature growth at low-seawater salinity and the best high-temperature growth at high salinity.

The effects of mangrove soil and root extract on the growth rates of six fungi, *Robillarda rhizophorae, Circinella simplex, Pycnidiophora multispora, Trichoderma viride, Cylindrocladium parvum*, and *Fusarium oxysporum*, were studied. The influence of mangrove soil and root extract on the fungal growth was selective. Generally, fungi isolated from the mangrove root grew best in the root-extract medium, whereas fungi isolated from the soil grew best in the soil-extract medium.

LITERATURE CITED

ALEXANDER, M. 1961. Introduction to soil microbiology. John Wiley and Sons, New York. 472 pp.

BARGHOORN, E. S., and D. H. LINDER. 1944. Marine fungi: their taxonomy and biology. Farlowia, vol. 1, pp. 395–467.

BISBY, C. R. 1943. Geographical distribution of fungi. Botanical Review, vol. 9, pp. 466–482.

BURGES, A., and F. RAW [eds.]. 1967. Soil biology. Academic Press, New York. 532 pp.

CHAPMAN, H. D., and P. F. PRATT. 1961. Methods of analysis for soils, plants and waters. University of California, Division of Agricultural Sciences. 309 pp.

COWLEY, G. T., and W. F. WHITTINGHAM. 1961. The effect of tannin on the growth of selected soil microfungi in culture. Mycologia, vol. 53, pp. 539–542.

GRAY, W., P. V. C. PINTO, and S. G. PATHAK. 1963. Growth of fungi in sea water medium. Applied Microbiology, vol. 11, pp. 501–505.

JAMES, N. 1958. Soil extract in soil microbiology. Canadian Journal of Microbiology, vol. 4, pp. 363–370.

JENSEN, W. A. 1962. Botanical histochemistry. W. H. Freeman and Co., San Francisco. 408 pp.

JONES, E. B. G., and D. H. JENNINGS. 1964. The effect of salinity on the growth of marine fungi in comparison with non-marine species. Transactions of the British Mycological Society, vol. 47, pp. 619–625.

KATZNELSON, H., A. G. LOCHHEAD, and M. T. TIMONIN. 1948. Soil microorganisms and the rhizosphere. Botanical Review, vol. 14, pp. 543–587.

KOHLMEYER, J. 1969. Ecological notes on fungi in mangrove forests. Transactions of the British Mycological Society, vol. 53, pp. 237–250.

LEE, B. K. H. 1971. Ecological and physiological studies of soil microfungi in Heeia mangrove swamp, Oahu, Hawaii. Unpublished Ph.D. dissertation, University of Hawaii, Honolulu. 103 pp.

LEWIS, J. A., and G. C. PAPAVIZAS. 1967. Effects of tannins on spore germination and growth of *Fusarium solani* f. *phaseoli* and *Verticillium albo-atrum*. Canadian Journal of Microbiology, vol. 13, pp. 1655–1661.

MORTON, J. F. 1965. Can the red mangrove provide food, feed, and fertilizer? Economic Botany, vol. 19, pp. 113–123.

PARKINSON, D., and J. S. WAID [eds.]. 1960. The ecology of soil fungi. Liverpool University Press, Liverpool. 324 pp.

PUGH, G. J. F., and J. NICOT. 1964. Studies on fungi in coastal soils V. *Dendryphiella salina*. Transactions of the British Mycological Society, vol. 47, pp. 263–267.

RITCHIE, D. 1957. Salinity optima for marine fungi affected by temperature. American Journal of Botany, vol. 44, pp. 870–874.

——— 1959. The effect of salinity and temperature on marine and other fungi from various climates. Bulletin of the Torrey Botanical Club, vol. 86, pp. 367–373.

RITCHIE, D., and M. K. JACOBSOHN. 1963. The effects of osmotic and nutritional variation on growth of a salt-tolerant fungus *Zalerion eistla*. In: C. H. Oppenheimer, ed., Symposium on marine microbiology, pp. 286–299.

Charles C Thomas, Publisher, Springfield, Illinois.

SWART, H. J. 1958. An investigation of the mycoflora in the soil of some mangrove swamps. Acta Botanica Neerlandica, vol. 7, pp. 741–768.

TESTRAKE, D. 1959. Estuarine distribution and saline tolerance of some Saprolegniaceae. Phyton, vol. 12, pp. 147–152.

VAARTAJA, O. 1960. Selectivity of fungicidal materials in agar cultures. Phytopathology, vol. 50, pp. 870–873.

WALSH, G. E. 1967. An ecological study of a Hawaiian mangrove swamp. In: G. H. Lauff, ed., Estuaries, pp. 420–431. Publications for the American Association for the Advancement of Science, no. 83, Washington, D. C.